HABITAT SELECTION STRATEGIES OF MOSQUITOES INHABITING CITRUS IRRIGATION FURROWS

G. ALAN CURTIS[1]

ABSTRACT. The mosquitoes *Aedes vexans, Psorophora columbiae* and *Psorophora howardii* have recently extended their habitat distribution into citrus irrigation furrows in coastal southeastern Florida. Oviposition site selection was examined by correlating species abundances with water depths due to rainfall or flood irrigation. *Psorophora columbiae* and *Ps. howardii* oviposited low in furrows, shared similar distributional relationships to water depths and were hatched by rainfall or irrigation. *Aedes vexans* oviposted higher in the citrus furrow, showed a different relationship to water depth and were hatched only by flood irrigation.

INTRODUCTION

Presence of mosquito larvae in any habit is determined entirely by maternal choice. Habitat selection is among the most important behavioral responses that the female mosquito makes, since the effect of this choice dictates the fate of her offspring. Successful choices by pioneering females may result in establishment of species in a newly exploitable environment (Curtis and Frank 1981) or perpetuate the species in an established habitat. If selected habitats contain inadequate food, abundant predators or insufficient water then few or weak individuals may result (Krebs 1972).

Successful mosquito establishment in man-made habitats is of particular interest. Species that are able to select and propitiously adapt to a man-made habitat have the possibility of exploiting a new environment, with few or no other mosquito species present. One of the commonest man-made mosquito habitats is that of land irrigated for agricultural purposes (Al-Azawi and Chew 1959, Boyd 1941, Briscoe 1952, Edmunds 1958, Gunstream and Chew 1964, 1967; Harden, et al. 1967, Hill et al. 1977, Portman 1954, Reeves and Hammon 1962, Shemanchuk 1959 and Surtees 1970a, 1970b). However, the mechanisms for mosquito establishment in man-made habitats are not well known.

Citrus groves in coastal southeastern Florida have been intensively cultivated since the early 1900s, but the numbers of associated mosquitoes have increased relatively recently (Curtis and Frank 1981). Much of this increased abundance is in response to the advent and widespread use of crown flood irrigation. In a previous study employing egg survey techniques, it was demonstrated that *Aedes vexans* oviposited in a specific region of the citrus furrow (Curtis and Frank 1981).

The present study describes some of the tactics for colonization and interspecies relationships used by mosquitoes inhabiting citrus irrigation furrows.

MATERIALS AND METHODS

Data presented here were collected from two similar 16.2 ha mature citrus groves located ca. 16.1 km apart in Indian River County, FL (27.5 N, 81.5 W). Each grove was cultivated by the same techniques, which included crown flood irrigation. A general grove description is given by Curtis and Frank (1981).

Biotic and abiotic data were collected from the 2 groves over a 5-year period (1978–82). Following rainfall or flood irrigation, immature mosquitoes were collected from 9 selected sites within the citrus grove, determined by a stratified random method. An open ended 0.25 m^2 box was forced into the bottom substrate and all larvae and pupae were removed for counting as earlier described (Curtis and Frank 1981). Collections were made daily as long as the aquatic habitat persisted. During each sampling occasion when sampling was conducted, water depth was recorded in association with mosquito species abundance, whether from rainfall or flood irrigation.

Soil samples for locational detection of mosquito eggs were collected as described by Curtis and Frank (1981). Samples were analyzed from 3 specific vertical stratifications of the citrus irrigation furrow, these being: (A) lower (bottom of furrow to 0.3 m vertical elevation), (B) middle (0.3 – 0.6 m elevation) and (C) upper section (0.6 – 0.9 m elevation) of the furrow (Fig. 1). From each location 30 random samples were processed and mosquito eggs identified.

The ability of rainfall or flooding to fill and persist in the furrow was evaluated by measuring water depth at randomly selected sites throughout the grove following rainfall or flooding. Sampling was continued as long as measurable water persisted in the habitat. For the purpose of correlating habitat persistence with a given rainfall, only the occasions when no

[1] Indian River Mosquito Control District, P.O. Box 670, Vero Beach, Florida, 32961.

intervening rainfall occurred were analyzed. Regression analysis on data to produce figures 2–5 was accomplished using a best fit program for linear and nonlinear data using least squares techniques (Daniel and Wood 1980).

RESULTS

The standard configuration for a citrus furrow in coastal Florida resembles a parabola with a height of 0.9 m and width of 7.6 m. Figure 1 depicts the amount of rainfall in 24 hr necessary to fill the furrow to various depths and the percentage of the total depth filled by rainfall. By design, crown-flood irrigation fills the furrow to 100% capacity, a value that would require over 43 cm of rainfall in 24 hr.

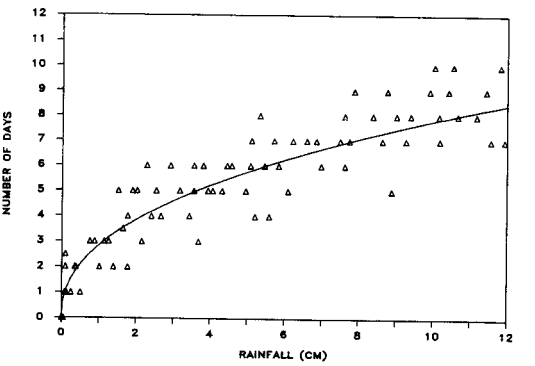

Fig. 2. Regression of rainfall and number of days that free water persisted in the furrow following specific rainfall amounts. Regression described by the equation, $y=ab^x$ ($R^2=0.862$, $n=125$).

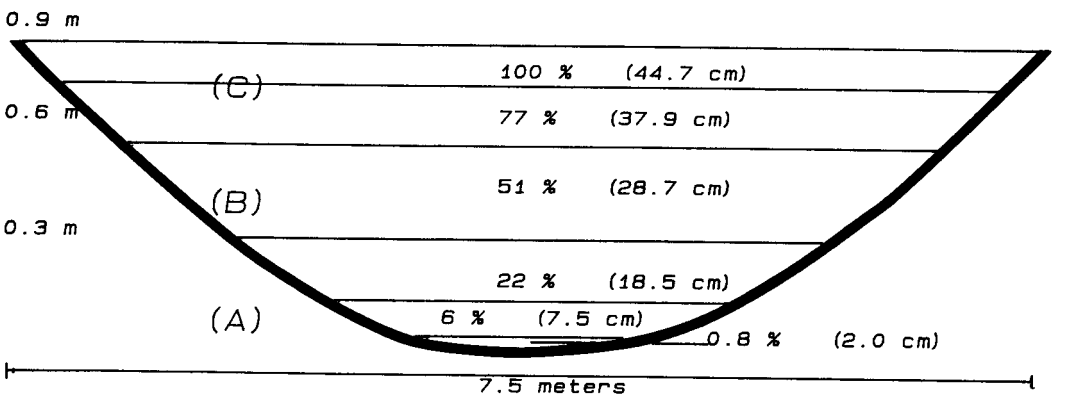

Fig. 1. Citrus furrow profile showing physical dimensions and relationship between furrow configuration and rainfall required to fill it to various depths. Vertical sections A, B and C designate areas used for special soil samples.

The relationship between amount of rainfall within 24 hr and persistence of water in the furrow is described by a power curve equation ($y = ab^x$, $R^2 = 0.862$, $P<0.001$) (Fig. 2). In contrast, standing water persists on average 17 days following flood irrigation.

During the study period, 119,518 *Aedes vexans* (Meigen), 43,376 *Psorophora columbiae* (Dyar and Knab) and 1,394 *Ps. howardii* Coquillett were collected in 1256 water samples. The abundance of each species showed a significant correlation with water depth, whether from rainfall or irrigation (figures 3–5). These species represented 97.3% of all mosquitoes collected during the course of study. Figures 3–5 represent the mean number/sample from the 9 collections/day following a specific rainfall or flood irrigation.

Excluded from the data are the occasions of rainfall or flooding during late December through May for *Ps. columbiae* and *Ps. howardii* when eggs of these mosquitoes are in a quiescent period.

Analysis of *Ae. vexans* eggs collected from soil samples gave means of 0.3, 2.0 and 43.3 eggs/sample from sections A, B and C respectively. The non-parametric rank comparison (Dunn's Multiple Comparison Technique (Dunn 1964)), concluded that section C, the uppermost region, contained significantly greater *Ae. vexans* egg numbers than the other 2 sections ($P<0.05$). *Psorophora columbiae* egg collections produced means of 5.2, 1.0 and 0.1 eggs/sample for sections A, B and C respectively. Statistical analysis confirmed that section A, the lowest region, contained significantly greater numbers of *Ps. columbiae* eggs than B or C ($P<0.05$). The mean number of eggs/sample for *Ps. howardii* was 1.93 for A, 0.33 for B and 0.10 for C with A being significantly greater than B or C($P<0.05$).

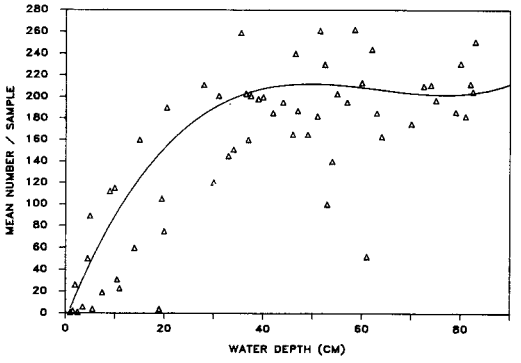

Fig. 3. Regression of water depth from either rainfall or flood irrigation and mean/sample of *Psorophora columbiae*. Regression described by cubic equation, $y=-23.6+11.9x-0.19x^2+0.001x^3$ ($R^2=0.86$, n=851). Samples during egg quiescent period have been excluded.

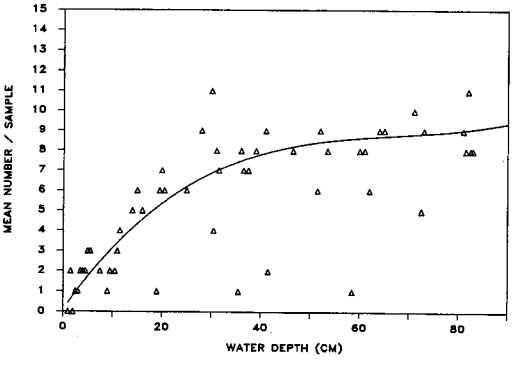

Fig. 4. Regression of water depth from either rainfall or flood irrigation and mean/sample of *Psorophora howardii*. Regression described by cubic equation, $y=0.08+0.4x-0.01x^2+2.4E-5x^3$ ($R^2=0.82$, n=851). Samples during egg quiescent period have been excluded.

The curvilinear relationship between water depth, whether from rainfall or flooding and *Ps. columbiae*, (Fig. 3) indicates that there is a relatively steady increase in mosquito numbers with increasing water depth to a level of approximately 35 cm, at which point the curve becomes asymptotic, as described by the cubic regression of water depth and *Ps. columbiae* ($y=-23.6+11.9x-0.19x^2+0.001x^3 R^2=0.86$). A third degree polynomial expression demonstrates a similar relationship for *Ps. howardii* ($y=0.08+0.4x-0.01x^2+2.4E-5x,^3$ $R^2=0.82$) with the exception that the asymptote begins at a slightly shallower depth than for *Ps. columbiae* (Fig. 4). A different association exists between water depth and *Ae. vexans* abundance ($y=0.95e^x$, $R^2=0.79$) (Fig. 5). Collections of

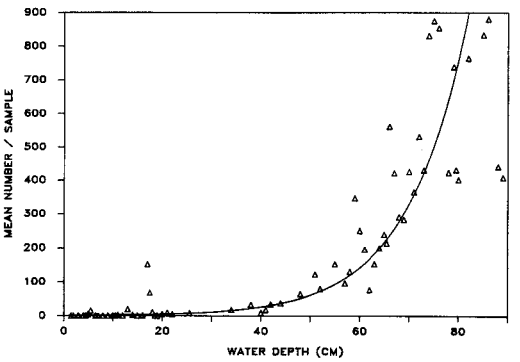

Fig. 5. Regression of water depth from either rainfall or flood irrigation and mean/sample of *Aedes vexans* is described by the equation, $y=0.95e^{0.08x}$ ($R^2=0.79$, n=1,256).

immature *Ae. vexans* remained low up to a depth of 50-60 cm whereupon a steep increase in *Ae. vexans* numbers was observed.

DISCUSSION

The successful exploitation of citrus groves by mosquitoes is a clear example of a man-made environment being colonized by indigenous species. In the case of *Ae. vexans*, an uncommon resident mosquito became abundant because it was able to take advantage of the recently created habitat (Curtis and Frank 1981). *Psorophora columbiae* and *Ps. howardii* have selected other regions of furrows to fit their specialized developmental needs. These microhabitats seem to mimic their traditional natural habitat.

Due to the ephemeral nature of the aquatic citrus furrow habitat, desiccation is the single largest contributor to mosquito mortality. Furrow construction is such that drainage is facilitated by a slight gradient along its length. Therefore, larvae residing at upper elevations along the furrow's length may face desiccation sooner than those in the lower end of the furrow. Desiccation was the principal cause of mortality in artificially flooded ponds as reported by Pritchard and Scholefield (1983). *Aedes vexans, Ps. columbiae* and *Ps. howardii* have minimized this risk by selecting differing oviposition sites that potentially insure larvae sufficient development time. McLachlan and Cantrell (1980) reported dipteran development time and habitat transience were positively correlated in rock pools.

The assumption that larval collections taken in association with varying water depths is an indicator of oviposition proved accurate. Albeit the method is indirect in comparison to egg

sampling, the statistical results (figures 3–5) allow little probability in making a type II error in acceptance of the wrong hypothesis. The regression equations for the three mosquito species all provided an excellent fit to the individual data sets. The profiles of water depth and mosquito abundance appear to be a good indicator of oviposition selection. Eggs collected from the soil samples corroborate the locations predicted by the regression analysis. Eggs of *Ae. vexans* were collected in the upper 30 cm of the furrows as also witnessed from the 1,256 larvae-water samples. Following rainfall, larvae of *Ps. columbiae* and *Ps. howardii* were most abundant in the lower 30 cm range. Eggs of these two species were similarly abundant in this same region. This distribution of larvae and eggs, as detected by hatching response to varying water depths and soil samples, illustrates female oviposition site selection within the citrus furrow habitat.

Both *Ps. columbiae* and *Ps. howardii* oviposit in the lower regions of the citrus furrows. Normal rainfall or flood irrigation will immerse eggs of these species. After eclosing, they progress rapidly to adults, with mean development times (and ranges) in citrus groves of 5.5(4.08–8.0) days and 4.5(3.5–8.0) days for *Ps. columbiae* and *Ps. howardii* respectively (Curtis, unpublished data). Since *Ps. howardii* is an obligate carnivore after the first instar, it must rely on the concomitant hatching of prey mosquitoes or face certain starvation or desiccation if temperature or insufficient prey extend development time beyond the habitat's permanence.

From figures 3 and 4 it is seen that *Ps. howardii* and *Ps. columbiae* peak in abundance at water depths of 30 and 35 cm respectively, equivalent to 14.8 cm and 17.3 cm of rainfall. Flooding by irrigation produces water depths between 60–90 cm, but does not increase numbers of *Ps. howardii* or *Ps. columbiae*. If these two mosquitoes used the entire available citrus furrow for oviposition, there would be a continuous increase in numbers with increasing water depths. *Psorophora columbiae* and *Ps. howardii* are using only about 20% of the available furrow surface area, specifically, the lower zone, that most likely to be inundated with normal rainfall.

Here, due to the parabolic shape of a furrow, mosquitoes encounter the moist, often saturated, soil. Such a substrate is highly attractive to ovipositing *Ps. columbiae* (Olson and Meek 1977, Al-Azawi and Chew 1959). Lower regions of the furrow are most similar to those of pastures and low lying environments commonly used by *Ps. columbiae* and *Ps. howardii*. Evidence for the similarities in egg distribution of *Ps. columbiae* and *Ps. howardii* is confirmed by using statistics that are sensitive to distributional characteristics and not abundance. The comparison of larvae collected in relation to water depth via the Kolmogorov-Smirnov test, demonstrated no significant difference in distributions between these two mosquitoes ($P > 0.25$).

The distribution of *Ae. vexans,* due to ovipositional selection, contrasts sharply with that of the *Psorophora* species. This flood plain mosquito (Horsfall et al. 1975) shows a pronounced exponential relationship to increasing water depths (Fig. 5). Relatively few individuals were collected after most rainfalls, whereas *Ae. vexans* were numerous after flood irrigation or the rare rainfalls in excess of 29 cm in 24 hr.

Aedes vexans exhibits the longest development time of these 3 floodwater species, with a mean of 8.0 days and range of 5.0–17.0 days in citrus groves (Curtis, unpublished data). Only rainfall in excess of 10.2 cm would assure this mosquito ample time for development (Fig. 2). Although 10.2 cm of rainfall might insure ample habitat duration, Fig. 1 illustrates that this amount of rainfall is not adequate to fill the furrow to *Ae. vexans* preferred zone (C). Here, other ovipositional cues, such as shading and leaf litter are more influential.

Comparison of *Ae. vexans* density at different water depths with that of *Ps. columbiae* and *Ps. howardii* demonstrated significant differences in distributions (Kolmogorov-Smirnov test $P<0.001$) among both *Psorophora* species and *Aedes vexans*. Previous results indicate that *Ae. vexans* selects oviposition sites in the leaf litter, high on the citrus furrow under the canopy of the citrus trees where egg hatch is only stimulated by crown flood irrigation or excessive rainfall (Curtis and Frank 1981). This permits a long development time from egg hatch. Water from flood irrigation persists an average of 17 days, occasionally in an excess of 20 days. This period is sufficient for successful metamorphosis of *Ae. vexans* even when lower water temperture slows advancement.

Aedes vexans may be collected at any time of the year when flood irrigation occurs, but eggs of *Ps. howardii* and *Ps. columbiae* do not respond to ordinary hatching stimuli between late December through early May. This quiescent period is advantageous, since egg hatch in response to normal winter rainfall would present eclosing larvae with an environment of cool water temperatures. The resulting development times would exceed the aquatic habitat's permanence, and result in death due to desiccation. Lower water temperatures would also slow the predatory rate of *Ps. howardii* even if sufficient prey were available, and rapid development of this predator is of paramount importance in an ephemeral aquatic habitat. *Psorophora columbiae* and *Ps. howardii* could cer-

tainly develop successfully in winter if egg hatch was stimulated by flood irrigation since habitat permanence would be sufficient. However, hatching could also be stimulated by normal rainfall which may not be sufficient to allow development when water temperatures are low.

By hatching almost exclusively in response to crown flood irrigation, *Ae. vexans* is able to compensate for increased development time during unfavorable winter conditions, since habitat duration is more permanent. Commonly seen is a 17-day development for *Ae. vexans* following irrigation in January, when daily water temperature in citrus furrows ranges between 4–18C°.

ACKNOWLEDGMENTS

I am grateful to D.B. Carlson, G. D. Dodd, J. H. Frank, L.P. Lounibos and G.F. O'Meara for their useful comments and criticism of the manuscript.

References Cited

Al-Azawi, A. and R. M. Chew. 1959. Notes of the ecology of the dark field mosquito *Psorophora confinnis*, in the Coachella Valley, California (Diptera: Culicidae). Ann. Entomol. Soc. Am. 52:345–351.

Boyd, M. F. 1941. A historical sketch of the prevalence of malaria in North America. Am. J. Trop. Med. 21:223–224

Briscoe, M. S. 1952. The relation of insects and insect-borne diseases to the vegetation and environment in Liberia. Ecology 33:187–214.

Curtis, G. A. and J. H. Frank. 1981. Establishment of *Aedes vexans* in citrus groves in southeastern Florida. Environ. Entomol. 10:180–182.

Daniel, C. and F. Wood. 1980. Fitting equations to data. John Wiley and Sons, New York.

Dunn, O. J. 1964. Multiple comparisons using rank sums. Technometrics 6:241–252.

Edmunds, L. R. 1958. Field observations on the habits and seasonal abundance of mosquito larvae in Scotts Bluff County, Nebraska (Diptera: Culicidae). Mosq. News 18:23–26.

Gunstream, S. E. and R. M. Chew. 1964. Contribution to the ecology of *Aedes vexans* (Diptera: Culicidae) in Coachella Valley, California, Ann. Entomol. Soc. Am. 57:383–387.

Gunstream, S. E. and R. M. Chew. 1967. The ecology of *Psorophora confinnis* (Diptera: Culicidae) in southern California II. Temperature and development. Ann. Entomol. Soc. Am. 60:434–439.

Harden, F. W., H. R. Hepburn and B. J. Ethridge. 1967. A history of mosquitoes and mosquito borne diseases in Mississippi, 1699–1965. Mosq. News 27:60–66.

Hill, M. N., J. A. Chandler and R. B. Highton. 1977. A comparison of mosquito populations in irrigated and non-irrigated areas of Kano Plains, Nyanza Province, Kenya, pp. 307–315. *In*: E. B. Worthington (ed.). Arid land irrigation in developing countries: Environmental effects and problems. Pergamon Press, Inc., Elmsford, NY.

Horsfall, W. R., R. J. Novak and F. L. Johnson. 1975. *Aedes vexans* as a flood-plain mosquito. Environ. Entomol: 4:675–681.

Krebs, C. J. 1972. Ecology: The experimental analysis of distribution and abundance, Harper and Row, New York.

McLachlan, A. J. and M. A. Cantrell. 1980. Survival strategies in tropical rainpools. Oecologia 47:344–351.

Olson, J. K. and C. L. Meek. 1977. Soil moisture conditions that are most attractive to ovipositing females of *Psorophora columbiae* in Texas ricelands. Mosq. News 37:19–26.

Portman, R.F. 1954. Control of mosquitoes in California ricefields. J. Econ. Entomol. 47:818.

Pritchard, G. and P. J. Scholefield. 1983. Survival of *Aedes* larvae in constant area ponds in southern Alberta (Diptera: Culicidae). Can. Entomol. 115:183–188.

Reeves, W.C. and W. McD. Hammon. 1962. Epidemiology of the arthropod-borne encephalitides in Kern County, California, 1943–1952. Univ. Calif. Publ. Public Health 4:1–256.

Shemanchuk, J.A. 1959. Mosquitoes in the irrigated areas of southern Alberta and their seasonal changes in abundance and distribution. Can. J. Zool. 37:899–912.

Surtees, G. 1970a. Large scale irrigation and arbivorus epidemiology, Kano Plain, Kenya. J. Med. Entomol. 7:509–517.

Surtees, G. 1970b. Effects of irrigation on mosquito populations and mosquito-borne diseases in man, with particular reference to ricefield extension. Int. J. Environ. Stud. 1:35–42.